Forage Yield of Smooth Bromegrass Collections from Rural Cemeteries

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ABSTRACT

Smooth bromegrass (*Bromus inermis* Leyss) is poorly adapted to management-intensive rotational grazing because of slow and limited regrowth potential. In an effort to discover germplasm with tolerance to frequent cutting, smooth bromegrass plants were collected from fence and sod habitats of 30 rural cemeteries in Iowa, Minnesota, and Wisconsin. The objective of this study was to quantify, describe, and test the responses of paired fence and sod populations to different harvest frequencies. Thirty sod populations, 30 fence populations, and five cultivars were evaluated for season-total forage yield and regrowth percentage at Arlington, WI, and Ames, IA. Three harvest managements were used, with mean harvest frequencies of four, five, or six harvests over 2002 and 2003. Fence populations had an average forage yield 5.5% higher than sod populations, a difference that was fairly consistent across harvest managements, test locations, and state of origin. Variation in linear responses to harvest management made up 65 and 77% of the harvest management × population interaction for forage yield and regrowth percentage, respectively. For seven cemetery sites, the sod population was better adapted than the fence population to a more frequent harvest management, as measured by a more stable response to harvest frequency (-2.02 ± 0.10 vs. -2.67 ± 0.12 Mg ha^{-1} harvest^{-1}). For nine cemetery sites, the sod population had a higher increase in regrowth percentage with increased harvest frequency (15.8 ± 0.5 vs. $11.9 \pm 0.7\%$ units harvest^{-1}). Smooth bromegrass germplasm from some cemetery sods appears to have potential value for developing tolerance to frequent defoliation.

SMOOTH BROMEGRASS is an important forage grass in much of temperate North America, used primarily for infrequent hay harvests, soil conservation, or other situations that are characterized by relatively low levels of management. It is preferentially adapted to hay management and favored by infrequent cutting, relatively high cutting heights, and high nitrogen fertility (Casler and Carlson, 1995). Smooth bromegrass is not well adapted to frequent defoliation (Casler et al., 1998; Smith et al., 1973). Unlike many other cool-season forage grasses, forage production of smooth bromegrass is not stimulated by defoliation, regardless of the growth stage (Harrison and Romo, 1994; Lawrence and Ashford, 1969). Smooth bromegrass stands decline under rotational grazing, an effect that is magnified by increasingly intensive grazing (Bittman and McCartney, 1994).

Regrowth and persistence of smooth bromegrass is limited by the timing of new tiller development. Development of new tillers in smooth bromegrass is largely determinant, with synchronized elevation and elongation of new apical meristems above the soil surface (Krause and Moser, 1977). Regrowth is reduced by cutting or grazing before new tillers have developed sufficiently, eventually reducing persistence (Eastin et al., 1964; Reynolds and Smith, 1962). During reproductive development, this critical time occurs from culm elongation to late heading. Cutting before culm elongation (to avoid removal of apical meristems) or well after heading (when new tillers have begun to emerge) leads to increased forage yields and persistence (McElgunn et al., 1972; Paulsen and Smith, 1968). Apical dominance in smooth bromegrass is strong until anthesis, when auxin activity declines and tillering is normally resumed (Eastin et al., 1964). Because smooth bromegrass produces true culms with elevated apical meristems on regrowth, timing of subsequent harvests may also be critical for smooth bromegrass regrowth and persistence. Regrowth of smooth bromegrass is not closely related to carbohydrate reserves in roots and crowns (Eastin et al., 1964; Paulsen and Smith, 1969; Raese and Decker, 1966; Reynolds and Smith, 1962).

The first widespread use of smooth bromegrass in the USA occurred during the drought of the 1930s when it was an important component of hay, pasture, and conservation plantings (Casler and Carlson, 1995). Remnants of these plantings can be found in rural areas throughout the central USA. Smooth bromegrass can persist in the soil in the form of seed or rhizomes, potentially leading to long-term persistence of remnant populations from plantings made in the 1930s.

Rural cemeteries are another source of smooth bromegrass germplasm that likely occurs as remnants of plantings from the 1930s. Many rural cemeteries of the North Central USA are characterized by a Kentucky bluegrass (*Poa pratensis* L.) sod that is well maintained by members of a local church or cemetery association. Smooth bromegrass often survives in both the cemetery sod and the area surrounding the cemetery. In many cases, the fence or border population of smooth bromegrass is unmanaged, creating two visually distinct habitats for smooth bromegrass: a frequently mowed sod and an uncut fence or border area. When compared in a common nursery, fence and sod populations from many cemeteries are phenotypically similar to each other, suggesting that they represent a single population that has not been modified by habitat management (Casler, 2004). Migration from the fence to the sod, either by rhizomes or seed, may also contribute to maintenance of genotypic diversity, but a similar overall phenotype in fence and sod populations. In other cases, there is clear phenotypic divergence between fence and sod populations, suggesting the possibility that natural selection

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may be responsible for a degree of genetic differentiation between them (Casler, 2004). Natural selection pressures appeared to be greater in sod populations than in fence populations, resulting in greater among-cemetery variability for sod vs. fence populations (Casler, 2004).

Because sod plants can only reproduce by rhizomes, natural selection pressure in the sod habitat would favor genotypes with a greater tolerance for frequent defoliation and greater long-term survivorship. Preliminary evidence for this was found in the observation that, for a limited number of cemeteries, the fence population had considerably higher forage yield than the sod population under infrequent harvest, but fence and sod populations were equal in forage yield under frequent harvest (Casler, 2004). The objective of this experiment was to quantify, describe, and test the responses of paired fence and sod populations to different harvest frequencies.

MATERIALS AND METHODS

Smooth bromegrass plants were collected from 30 cemeteries in Minnesota, Wisconsin, and Iowa in 1995 and 1996. Details of the collection protocol and location of the cemeteries are provided by Casler (2004). Smooth bromegrass plants were collected only from cemeteries with the following characteristics: (i) a well-managed turf, dominated by Kentucky bluegrass, with few obvious weeds and showing no evidence of infrequent or lax mowing management, (ii) a reasonably vigorous stand of smooth bromegrass in the sod, and (iii) a good stand of uncut smooth bromegrass in the fence or border area. Plants were collected from the fence and sod of each cemetery, creating discreet populations of smooth bromegrass plants. Each population was phenotypically similar to the southern (steppe) type of smooth bromegrass.

In 1999, 25 random plants of each population (one habitat of one cemetery) were cloned into four replicates and transplanted into one of 60 isolated crossing blocks at Arlington, WI. Each crossing block contained 25 clones of a population and four replicates in a randomized complete block design with a 0.6-m plant spacing. Each crossing block was 10 m from the adjacent crossing block and winter rye (*Secale cereale* L.) was planted as a pollen barrier between all crossing blocks in autumn 1999. Seed was harvested from each plant in July 2000, threshed, cleaned, and bulked in equal volumes for all plants within a crossing block. Seed was tested for germination using standardized methodology in February 2001 (AOSA, 1998).

In April 2001, three separate experiments were planted at Ames, IA, and Arlington, WI. The soil types were Plano silt loam (fine-silty, mixed, mesic Typic Argiudoll) at Arlington and Nicollet loam (fine-loamy, mixed, mesic Aquic Hapludoll) at Ames. The seeding rate was 600 pure live seeds m^{-2}, which was equivalent to an average seeding rate of 22 kg ha^{-1}. Each experiment was designed as a randomized complete block with four replicates. Plot size was 0.9×1.5 m with five drilled rows. Five check cultivars were also included in each experiment.

The three experiments were designed for three harvest managements, originally designated as two harvests per year (anthesis and post-killing-frost), three harvests per year (early heading, 30-cm canopy, and post-killing-frost), or four harvests per year (30-cm canopy at each harvest date). Because of mild drought in 2002 and severe drought in 2003, harvest frequencies were compressed to the following three treatments, spanning 2002 and 2003: four harvests (as originally planned), five harvests (three as planned in 2002 but only the first two harvests in 2003), and six harvests (Arlington: four

as planned in 2002 but only the first three in 2003; Ames: the first three harvests in 2002 and the first two harvests in 2003). The six-harvest treatment represents an average number of harvests over the two locations (seven at Arlington and five at Ames). Because the growth stages and timing of the harvests were similar between the two locations, they differed largely in the presence or absence of the later harvests when the effects of drought were most severe.

Nitrogen fertilizer was applied early in the spring and immediately after each harvest (except the last harvest within each year) at the following rates: 112 kg N ha^{-1} (four-harvest treatment), 75 kg N ha^{-1} (five-harvest treatment), and 56 kg N ha^{-1} (six-harvest treatment). Nitrogen rates were originally intended to be equal, on a season-total basis, across the three harvest managements, but loss of some harvests on the two most frequent harvest managements eliminated some of the nitrogen applications. This created a small amount of confounding between harvest managements and total nitrogen application rates, resulting in less nitrogen applied as the frequency of harvest increased. However, because cultivar $\times$ nitrogen-fertilization-level interactions are biologically unimportant in smooth bromegrass (Fortmann, 1953; Offutt and Hileman, 1972), this confounding should not affect the interpretation of population $\times$ harvest management interactions.

Each experiment was harvested according to the harvest management described above, with a flail harvester at Arlington and a sickle-bar harvester at Ames. Because all populations had similar maturity on any given harvest date, dry matter was determined on a bulk sample of harvested forage from 14 plots and a single dry matter value was used to adjust all plot biomass values to a dry-matter basis. We justified this procedure on the basis of previous work that demonstrated little or no genetic variation for maturity or dry matter content of smooth bromegrass (Casler et al., 2000) and the fact that each block could be harvested within 30 to 40 min, minimizing any dirunal changes in dry matter content. Samples were dried at 60°C before dry matter determination. Although ground cover (persistence) was one of the intended variables for measurement, there was no observable loss of ground cover for the duration of the experiment in any of these populations.

Forage yield data for each harvest were analyzed by nearest neighbor analysis to adjust each plot value for spatial variation, using the two-covariate, preadjustment-by-harvests method of Smith and Casler (2004). Spatial adjustment decreased effective error mean squares by 0 to 107% (average of 24%) and the spatial covariates accounted for 0 to 31% (average of 10%) of the plot-to-plot variability. Regrowth percentage was computed for each plot in each growing season using adjusted plot forage yield values. Regrowth was defined as total forage yield for all harvests following the first harvest within a growing season.

Spatially adjusted season total forage yield and regrowth percentage were analyzed by analysis of variance in which all factors (years, locations, harvest managements, and populations) were assumed to have fixed effects, except replicates. Years were considered fixed because of age of stand and dominance of drought effects. Locations were considered fixed because they each represented one site within the geographic range of the Iowa and Wisconsin cemetery collection sites. The main effect of populations was partitioned into sources of variation describing the structure of the populations: habitat, (1 df), cemetery (29 df), and habitat $\times$ cemetery (29 df). The interactions of populations with locations and years were similarly partitioned.

The population $\times$ harvest management interaction was partitioned into single-degree-of-freedom contrasts to measure the linear effect of harvest management on each population

by the methods of Hill and Baylor (1983). For each of the 30 cemeteries, three orthogonal contrasts were computed: (i) the linear regression of fence population means on the number of harvests over the 2-yr period, (ii) the linear regression of sod population means on the number of harvests over the 2-yr period, and (iii) the linear response × habitat interaction, which measures the difference in slope between (i) and (ii). Linear regressions on the number of harvests over the 2-yr period were also computed for each of the five cultivars.

RESULTS AND DISCUSSION

Population × year interactions were always considerably smaller than population × location interactions and population main effects. While some population × year interaction terms were statistically significant, interpretation of results did not change between years, indicating that these interactions were of little biological significance. Therefore, all results are presented as means over 2 yr. Only two portions of the population × location interaction were significant, the location × state-of-origin and the location × site within state-of-origin interactions. Habitat did not interact with location. Results are presented as means over locations or within locations, depending on the relative importance of these portions of the population × location interaction. Higher-order interaction terms were not significant.

Forage yield declined with increased harvest frequency, by -1.35 ± 0.15 Mg ha^{-1} harvest^{-1} at Arlington ($P = 0.04$) and by -3.17 ± 0.04 Mg ha^{-1} harvest^{-1} at Ames ($P < 0.01$). These linear responses accounted for over 99% of the variability in mean forage yield across harvest managements. These responses were largely a result of the significant reductions in first-harvest forage yield associated with the earlier harvest date and the lower N applications in early spring of the more frequent harvest managements: -2.06 ± 0.01 Mg ha^{-1} harvest^{-1} at Arlington ($P < 0.01$) and -2.59 ± 0.05 Mg ha^{-1} harvest^{-1} at Ames ($P < 0.01$). The average dates of first harvest were 26 May (jointing), 6 June (early heading), and 12 June (anthesis) for the 4-, 5-, and 6-harvest treatments, respectively (SE = 2 d). At the rates of nitrogen applied in this study, which were similar for the entire season across harvest managements, smooth brome-

grass was incapable of recovering lost forage yield potential associated with earlier spring harvest.

The forage yield responses to harvest management were reflected in changes in regrowth percentage across harvest managements, which increased by $21.2 \pm 2.6\%$ units harvest^{-1} at Arlington ($P = 0.04$) and $5.6 \pm 1.1\%$ units harvest^{-1} at Ames ($P = 0.06$). The lower response of regrowth percentage to increasing harvest frequency at Ames indicated that plots under a more frequent harvest management were much less capable of responding with increased regrowth percentage at Ames compared to Arlington. This may be an indication that the drought experienced at both sites in both years was more severe at Ames than at Arlington. In both years at both locations, drought severity increased through the growing season, becoming more pronounced after the summer solstice. Thus, regrowth forage yields were more severely affected by drought than first-harvest forage yields.

Cemetery populations derived from the three states of origin were similar in forage yield at Arlington (5.68–5.87 Mg ha^{-1}) but differed at Ames (Table 1). At Ames, Iowa populations had 8.2% higher forage yield than those from Wisconsin and Minnesota (9.74 vs. 9.00 Mg ha^{-1}; $P < 0.01$). This result suggested that populations collected in Iowa may be better adapted to Ames than to Arlington. Because most of the Iowa cemeteries were clustered around Ames, this may be evidence of an adaptive response as populations evolved at these cemeteries. While fence populations may be relatively stable because of low or nil immigration rates and lack of obvious natural selection pressures, sod populations are subject to immigration and natural selection (Casler, 2004). It is possible that natural selection pressures on smooth bromegrass populations at Iowa cemeteries may have resulted in adaptive shifts to some factor characterizing the local environment, but it is not realistic at this time to speculate on the identity or nature of this factor.

Perennial grasses are capable of adaptive genetic shifts in response to local environmental conditions. Natural selection pressures on perennial grasses can create differential adaptive changes across distances as short as 1 m (Snaydon, 1970). Population differentiation can result from spatial variation in defoliation frequency, soil type,

Table 1. Mean season total forage yield of smooth bromegrass populations collected from fence or sod habitats of rural cemeteries in Iowa, Minnesota, or Wisconsin and evaluated under three management regimes (four, five, or six harvests over a 2-yr period) at two locations.

Source of germplasm†	Arlington, WI			Ames, IA			Mean
	Four harvests	Five harvests	Six harvests	Four harvests	Five harvests	Six harvests	
	Mg ha^{-1}						
Iowa							
Fence	7.48**	5.95**	4.71**	13.36**	9.94**	6.65*	8.01*
Sod	7.12	5.55	4.43	12.78	9.33	6.37	7.60*
Minnesota							
Fence	7.62**	5.76*	4.73**	12.57**	9.16*	6.10*	7.66*
Sod	6.96	5.57	4.39	11.73	8.83	5.81	7.21*
Wisconsin							
Fence	7.46**	5.63**	4.60**	12.32**	9.11*	5.89	7.50*
Sod	6.75	5.30	4.34	11.90	8.79	5.76	7.14*

* Fence and sod means within a pair are significantly different at $P < 0.05$.
** Fence and sod means within a pair are significantly different at $P < 0.01$.
† Number of cemeteries: Iowa (9), Minnesota (9), Wisconsin (12).

soil nutrient levels, and the incidence of plant pathogens (Casler, 2004; Snaydon, 1987; Snaydon and Davies, 1972). Soil and/or climatic factors may have caused adaptive changes in remnant cemetery populations of smooth bromegrass, resulting in adaptive responses to local environments. Phenotypic plasticity, the ability of a plant to utilize different growth habits and/or strategies in response to its local environment (Sultan, 1987), is partially responsible for the differential phenotype of fence and sod populations in their original habitats. However, the presence of genotypic variability indicates that natural selection and/or differential origin of some populations are important phenomena contributing to differentiation of smooth bromegrass cemetery populations.

Fence populations had an average forage yield 5.5% higher than sod populations, a difference that was fairly consistent across harvest managements, test locations, and state-of-origin (Table 1). This difference accounted for 17% of the variation in forage yield among the 60 populations. There was a general trend for forage yield of fence and sod populations to converge as harvest frequency increased at Ames, perhaps reflecting reduced genotypic variability associated with drought-suppression of regrowth forage yields at Ames. However, taken as a whole, these results provide strong evidence that smooth bromegrass populations derived from cemetery sods have reduced forage yield potential compared with populations derived from fence rows surrounding these cemeteries. This result is similar to that observed in preliminary evaluations of the parents of these populations in which it was demonstrated that sod plants had shorter heights, narrower crown diameter, and lower forage yield (Casler, 2004). The consistency of these results across most cemetery sites suggests the presence of selection pressures toward a more prostrate sod phenotype and/or a more upright and vigorous fence phenotype. If differential origin of fence and sod populations was important, this effect would result in more-or-less random or unpredictable differences between fence and sod phenotypes in these uniform experiments.

Cemetery sites accounted for 62% of the variation in forage yield among the 60 populations. Mean forage yield ranged from 6.64 to 8.15 Mg ha^{-1} among the 30 cemetery sites. Most of these values were within the range of variability for the three cultivars with the lowest mean forage yield (Peak, Radisson, and Rebound with means of 8.01, 8.06, and 7.65 Mg ha^{-1}, respectively) but lower than the means for Alpha and Lincoln at 8.45 and 8.31 Mg ha^{-1}, respectively. Alpha and Lincoln are consistently high in forage yield among smooth bromegrass cultivars (Casler et al., 2000). These results indicate that the majority of germplasm collected from these cemeteries is relatively low in forage yield potential and it may require many years of selection and breeding to increase its forage yield potential to be competitive with the best cultivars available.

Results for regrowth percentage were less consistent than for total forage yield (Table 2). Differences between fence and sod populations were highly inconsistent, accounting for less than 1% of the variability in regrowth percentage among the 60 populations, suggesting that it is not possible to generalize differences in regrowth percentage between habitats. Cemetery sites accounted for 56% of the variation in regrowth percentage among the 60 populations. Mean regrowth percentage ranged from 33.0 to 38.7% among the 30 cemetery sites, with most sites falling within the range of cultivar means (33.9–37.0%). Populations from Minnesota had the highest regrowth percentage compared to populations from Iowa and Wisconsin (36.1 vs. 34.9%; $P < 0.01$).

Variation in linear responses to harvest management made up 65% of the harvest management × population interaction for forage yield ($P < 0.01$). Averaged over locations, fence populations ranged from −3.03 to −1.71 Mg ha^{-1} harvest^{-1} and sod populations ranged from −2.52 to −1.52 Mg ha^{-1} harvest^{-1} in their response to increasing harvest frequency (Table 3). Cemetery sites accounted for 39% of the variation among the 60 populations, which was reflected in a positive correlation between fence and sod responses ($r = 0.27$, $P < 0.05$). Habitat accounted for only 4% of this source of variation, reflecting a small, but statistically significant effect (−2.34 vs. −2.18 Mg ha^{-1} harvest^{-1} for fence vs. sod, respectively, $P < 0.01$).

Nevertheless, the large amount of variation among cemetery sites indicated that such generalizations cannot be extended to each population or site. For nine of the 30 cemeteries, the linear response of forage yield

Table 2. Mean regrowth percentage of smooth bromegrass populations collected from fence or sod habitats of rural cemeteries in Iowa, Minnesota, or Wisconsin and evaluated under three management regimes (four, five, or six harvests over a 2-yr period) at two locations.

Source of germplasm†	Arlington, WI			Arlington, WI			
	Four harvests	Four harvests	Mean	Four harvests	Four harvests	Four harvests	Mean
	Mg ha^{-1}						
Iowa							
Fence	16.6	28.8	54.9	30.7	38.2**	40.8*	35.0
Sod	16.2	28.5	55.5	29.2	35.7	37.9*	33.8
Minnesota							
Fence	16.6**	29.8	58.5*	32.0**	38.8*	42.5	36.4
Sod	13.4	29.8	60.1	29.0	40.6	41.7	35.8
Wisconsin							
Fence	15.3**	28.5	56.5**	30.4	38.2	41.3	35.0
Sod	13.6	28.5	60.1	29.1	39.6	42.3	35.5

* Fence and sod means within a pair are significantly different at $P < 0.05$.
** Fence and sod means within a pair are significantly different at $P < 0.01$.
† Number of cemeteries: Iowa (9), Minnesota (9), Wisconsin (12).

Table 3. Linear regression coefficients for the regressions of season total forage yield or regrowth percentage on the average number of harvests over 2 yr for 60 smooth bromegrass populations collected from fence or sod habitats in 30 rural cemeteries of Wisconsin (WI), Minnesota (MN), or Iowa (IA) and five smooth bromegrass cultivars. Values reported are based on means over two locations and 2 yr.

State	Site	Season total forage yield			Regrowth percentage		
		Fence†	Sod	P value‡	Fence	Sod	P value
WI	1	−2.39 ± 0.26	−2.16 ± 0.22	0.2432	11.9 ± 2.8	13.3 ± 0.3	0.2343
WI	2	−2.49 ± 0.12	−2.17 ± 0.25	0.0974	13.3 ± 2.2	16.1 ± 0.3	0.0170
WI	3	−1.94 ± 0.08	−2.52 ± 0.16	0.0032	16.0 ± 0.7	11.4 ± 0.4	0.0001
WI	4	−3.03 ± 0.60	−2.38 ± 0.21	0.0008	10.6 ± 0.9	13.4 ± 2.5	0.0170
WI	5	−2.36 ± 0.04	−2.08 ± 0.15	0.1450	12.0 ± 1.6	13.6 ± 0.8	0.1817
WI	6	−2.38 ± 0.04	−1.81 ± 0.05	0.0031	13.1 ± 0.6	16.6 ± 1.1	0.0025
WI	7	−1.92 ± 0.17	−2.43 ± 0.27	0.0082	16.3 ± 1.0	17.6 ± 0.9	0.2698
WI	8	−2.29 ± 0.17	−2.05 ± 0.32	0.2289	16.0 ± 2.5	16.0 ± 0.9	0.9913
WI	9	−1.71 ± 0.12	−1.52 ± 0.17	0.3116	14.4 ± 1.2	15.4 ± 3.2	0.3858
WI	10	−2.63 ± 0.11	−2.16 ± 0.32	0.0145	7.6 ± 2.1	14.5 ± 1.5	0.0000
WI	11	−2.16 ± 0.01	−1.93 ± 0.02	0.2353	12.6 ± 0.8	18.3 ± 1.7	0.0000
WI	12	−2.57 ± 0.05	−2.47 ± 0.13	0.6270	12.6 ± 2.4	12.8 ± 2.2	0.8955
MN	13	−2.48 ± 0.13	−2.38 ± 0.19	0.6043	10.3 ± 1.9	10.6 ± 0.3	0.7695
MN	14	−1.94 ± 0.13	−1.87 ± 0.16	0.7239	13.8 ± 2.7	16.8 ± 2.5	0.0101
MN	15	−2.64 ± 0.13	−1.76 ± 0.22	0.0000	13.4 ± 2.2	15.4 ± 1.6	0.0934
MN	16	−2.26 ± 0.02	−2.43 ± 0.05	0.4074	14.2 ± 2.2	15.9 ± 0.4	0.1574
MN	17	−2.41 ± 0.35	−2.45 ± 0.11	0.8258	15.3 ± 1.1	13.6 ± 1.5	0.1441
MN	18	−2.38 ± 0.75	−1.54 ± 0.41	0.0000	12.2 ± 2.1	16.6 ± 1.1	0.0002
MN	19	−1.93 ± 0.08	−1.96 ± 0.06	0.8929	13.3 ± 1.6	15.2 ± 0.3	0.1013
MN	20	−2.25 ± 0.36	−2.32 ± 0.22	0.7020	13.7 ± 0.8	16.0 ± 1.5	0.0461
MN	21	−2.76 ± 0.30	−2.39 ± 0.05	0.0595	11.8 ± 1.7	13.8 ± 2.7	0.0998
IA	22	−3.03 ± 0.01	−2.30 ± 0.16	0.0002	11.7 ± 1.4	13.1 ± 0.3	0.2143
IA	23	−2.04 ± 0.10	−1.97 ± 0.15	0.7151	13.1 ± 0.2	11.6 ± 0.8	0.1979
IA	24	−2.61 ± 0.38	−2.17 ± 0.29	0.0242	10.8 ± 1.4	11.6 ± 2.0	0.4985
IA	25	−2.54 ± 0.04	−2.37 ± 0.11	0.3871	10.5 ± 2.0	13.5 ± 3.4	0.0106
IA	26	−2.20 ± 0.38	−2.45 ± 0.15	0.1893	13.5 ± 2.5	11.8 ± 2.7	0.1498
IA	27	−1.87 ± 0.20	−2.22 ± 0.51	0.0698	14.6 ± 0.8	11.2 ± 1.4	0.0034
IA	28	−2.14 ± 0.35	−2.50 ± 0.12	0.0672	13.5 ± 0.2	12.2 ± 2.7	0.2784
IA	29	−2.33 ± 0.42	−2.06 ± 0.11	0.1614	10.0 ± 1.3	10.9 ± 1.6	0.4339
IA	30	−2.58 ± 0.32	−2.45 ± 0.19	0.4794	11.1 ± 2.6	11.9 ± 0.7	0.4742

† Standard errors were computed from the linear regressions on number of harvests over 2 yr (1 df).
‡ P value for fence vs. sod linear regression coefficients obtained by contrast F tests in ANOVA.

to harvest frequency differed between habitats at $P < 0.05$ (Table 3). For seven of these nine sites, the sod population had a greater slope (value closer to zero) than the fence population (Fig. 1). The net result for these seven sites was a superiority of the fence population under the four-harvest management and a gradual convergence of responses to the six-harvest management, with a reversal of ranking occurring at Sites 6 and 18. These results indicate that, for seven cemetery sites, the sod population was more stable across the three harvest managements. Several of these sod populations had linear responses that were higher (closer to zero) than for all or most of the five cultivars, most notably for Sites 15 and 18. These results further suggest that natural selection is likely a more important phenomenon than differential origin of fence and sod populations, which would have resulted in more random or less predictable differences between fence and sod populations.

Variation in linear responses to harvest management made up 77% of the harvest management × population interaction for regrowth percentage ($P < 0.01$). Fence populations ranged from 7.6 to 16.3% units harvest^{-1} and sod populations ranged from 10.6 to 18.3% units harvest^{-1} in their response to increasing harvest frequency (Table 3). Cemetery sites accounted for 45% of the variation among the 60 populations, which was reflected in a positive correlation between fence and sod responses ($r = 0.32$, $P < 0.05$). Habitat only accounted for 7% of this source of variation, reflecting a small, but statistically significant effect (12.8 vs. 14.0% units harvest^{-1} for fence vs. sod, respectively, $P < 0.01$).

As observed for forage yield per se, the variability among cemetery sites was large and significant. For 11 of the 30 cemeteries, the linear response of regrowth percentage to harvest frequency differed between habitats at $P < 0.05$ (Table 3). For nine of these 11 sites, the sod population had a greater slope than the fence population (Fig. 2). Thus, for these nine sites, the sod population responded more favorably to harvest frequency, with a greater increase in regrowth percentage than the respective fence population. Numerous sod populations and a small number of fence populations had linear responses of regrowth percentage to harvest frequency that numerically exceeded that of Radisson, the cultivar with the highest linear response for regrowth percentage. For four sites (4, 6, 10, and 18), the sod population had a more favorable response than the fence population to harvest frequency for both forage yield and regrowth percentage. A greater increase in regrowth percentage with increasing harvest frequency would be expected for sod populations, resulting from their more prostrate growth habit, if natural selection is responsible for differentiation between fence and sod populations.

Differential responses to harvest frequency of parents (Casler, 2004) and progeny populations (Table 3; Fig. 1 and 2) were manifested as more stable and uniform forage yield across harvest frequencies, i.e., a greater tolerance to frequent harvest in some sod populations and
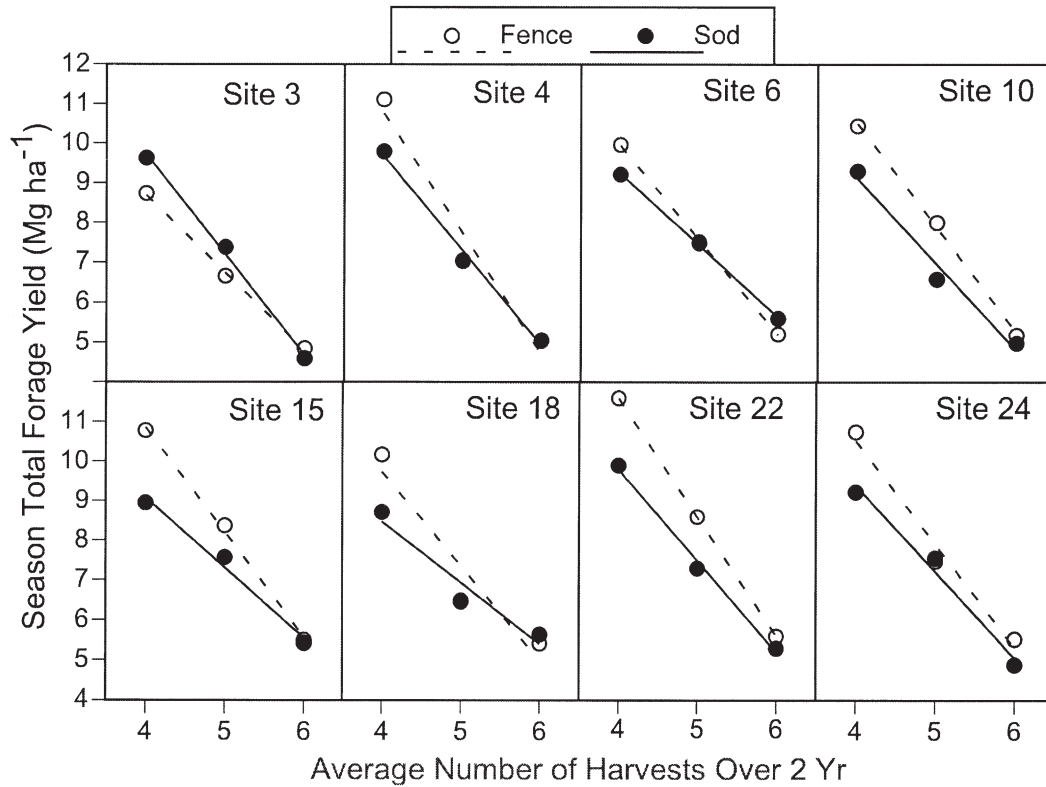
Fig. 1. Linear regressions of mean season total forage yield, over two locations and 2 yr, on average number of harvests over the 2-yr period for fence and sod populations of smooth bromegrass collected from eight rural cemeteries. Slopes for the linear regressions are shown in Table 3.
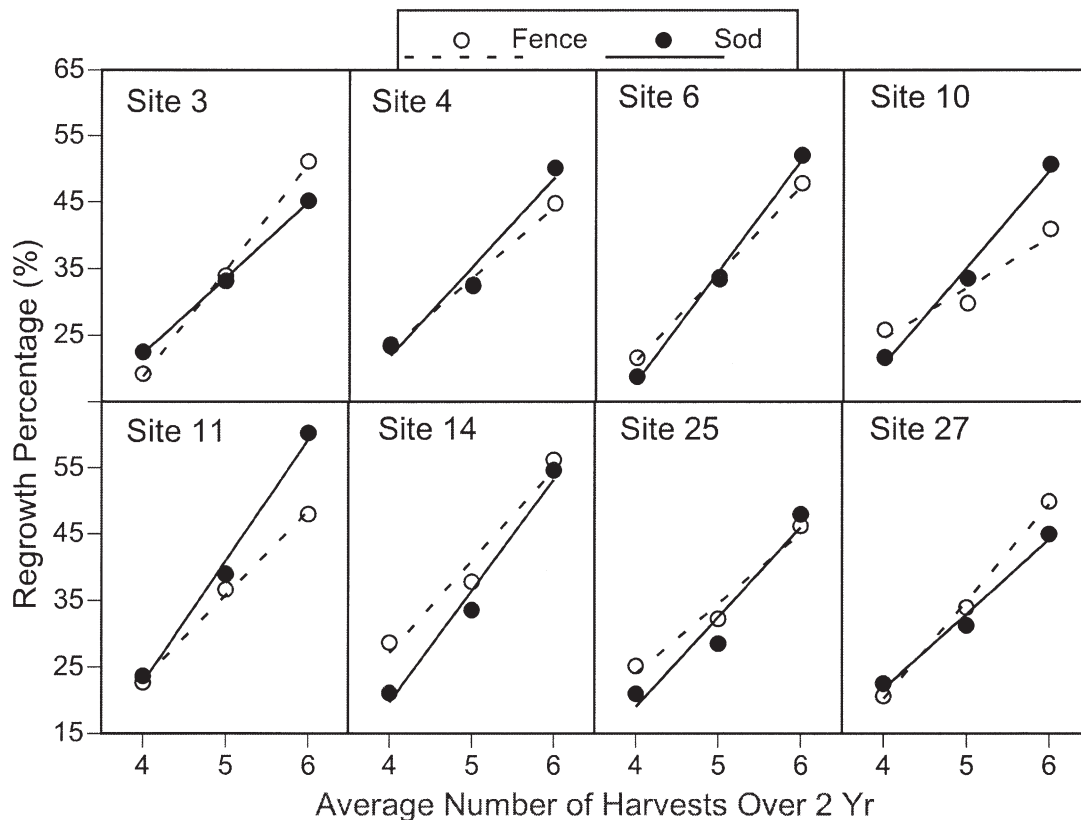

Fig. 2. Linear regressions of mean regrowth percentage, over two locations and 2 yr, on average number of harvests over the 2-yr period for fence and sod populations of smooth bromegrass collected from eight rural cemeteries. Slopes for the linear regressions are shown in Table 3.

less tolerance to frequent harvest in some fence populations. These responses indicate that there are natural selection pressures in rural cemeteries which have resulted in adaptive changes to smooth bromegrass remnant populations. Defoliation, particularly frequent defoliation that occurs in these cemetery sods, creates a stressful environment for perennial grasses (Harris, 1978; Snaydon, 1987). Perennial grasses, including smooth bromegrass, can undergo relatively rapid genetic changes in response to frequent defoliation (Falkner and Casler, 2000; Vaylay and van Santen, 1999).

CONCLUSIONS

Previous work suggests that sod populations are subject to selection pressure for survival under the frequent mowing management of rural cemeteries (Casler, 2004). This selection pressure appears to have resulted in some genetic shifts toward a more stable forage yield across harvest managements, most likely as a result of mortality of genotypes intolerant of frequent mowing. Conversely, fence populations are likely subject to selection pressure in the opposite direction, manifested as mortality of genotypes better adapted to a frequent mowing regime. This disruptive selection to differential management appears to be responsible for divergence of fence and sod populations at some rural cemetery sites. This divergence is balanced by migration from the fence population to the sod population, most likely by direct rhizome ingression along the boundary between the fence and sod and/or by seed dispersal and seedling recruitment under sparse cover or following the establishment of new graves. At some cemetery sites, characterized by homogeneous fence and sod populations, migration and selection appear to be balanced in a quasi-equilibrium state. Some of these sod populations, particularly those with higher forage yield and regrowth percentage under the highest harvest frequency, represent a valuable germplasm resource for improving tolerance to frequent defoliation in commercial smooth bromegrass.

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